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An unexpected discovery of hidden diversity: a new species of the genus *Calamaria* H. Boie in F. Boie, 1827 (Squamata, Calamariidae) from Guangxi, China

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Abstract

As part of our investigations into the systematics of the *Calamaria pavimentata* species complex, we describe a new species of the genus *Calamaria* from Chongzuo and Guilin Cities, Guangxi, China, based on a combination of morphological and molecular evidence. Morphologically, *Calamaria incredibilis* **sp. nov.** is distinguished from other congeners by the following combination of morphological characters: nine enlarged maxillary teeth; rostral higher than wide; prefrontal shorter than frontal and contacting the first two supralabials; mental not in contact with anterior chin shields; dorsal scales in 13–13–13 rows, smooth throughout; a single preocular and postocular; four supralabials, with the 2nd and 3rd ones contacting the eye; five infralabials; six scales surrounding the paraparietal; 170–182 ventrals in males; 21–23 paired subcaudals in males; a relatively short tail (8.2–8.4% of total length in males), thick and nearly cylindrical, gradually tapering to an obtuse point; dorsal coloration brown, seven longitudinal series of interrupted dark brown stripes are visible along the body, extending from behind the pale-colored collar to the tip of the tail; the margins of the dorsal scales are heavily suffused with black pigment, forming an almost reticulate pattern; the ventral surface yellowish white, with dark brown blotches along the outermost lateral margins; the absence of light spots on the dorsal tail. Phylogenetic analyses based on mitochondrial cytochrome *b* sequences recover *Calamaria incredibilis* **sp. nov.** as a well-supported independent lineage, forming a sister relationship with a subclade comprising *C. andersoni* Yang & Zheng, *C. synergis* Zhang, Xu, Nguyen, Poyarkov, Vogel, Wang & Huang, and *C. yunnanensis* Chernov. The new species is separated from its closest relatives by substantial mitochondrial genetic divergence (*p*-distance 12.67% based on cytochrome *b* gene). The discovery of *Calamaria incredibilis* **sp. nov.** further highlights the underestimated diversity within the *C. pavimentata* species complex and underscores the importance of integrative taxonomic approaches for resolving cryptic diversity in morphologically conservative, semi-fossorial snake lineages from southern China, with Guangxi emerging as an important hotspot of cryptic diversification.

Key Words

Calamaria incredibilis sp. nov., *C. pavimentata*, morphology, mtDNA, taxonomy

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Introduction

The genus *Calamaria* H. Boie in F. Boie, 1827, comprises small, semi-fossorial snakes distributed across northeastern India, mainland Southeast Asia, the Greater Sunda Islands, the Philippines, and several species pass Wallace's line and inhabit Sulawesi and the Maluku Islands (Uetz et al. 2026). To date, nine species have been recorded in China, including *C. arcana* Yeung, Lau & Yang; *C. andersoni* Yang & Zheng; *C. berezowskii* Günther; *C. jinggangensis* Cai, Jiang, Wu, Huang, Fei & Ding; *C.* cf. *pavimentata* Duméril, Bibron & Duméril; *C. septentrionalis* Boulenger; *C. similis* Qi, Nguyen, Yang, Xu, David, Shi, Liu, Rong, Korolev, Poyarkov & Wang; *C. synergis* Zhang, Xu, Nguyen, Poyarkov, Vogel, Wang & Huang; and *C. yunnanensis* Chernov (Cai et al. 2023; Liang et al. 2024a; Qi et al. 2026; Uetz et al. 2026). Notably, six species have been described or revalidated in the past decade, revealing that the diversity and taxonomy of *Calamaria* in China remain incompletely understood (Zhang et al. 2025a; Qi et al. 2026). Due to their secretive behavior and conservative external morphology, species boundaries within *Calamaria* have long been difficult to define.

One of the most challenging species in this genus is *Calamaria pavimentata* Duméril, Bibron & Duméril, 1854. Originally described from Java Island, Indonesia, its type locality has been questioned because no confirmed records of *C. pavimentata* have been found on the island (Inger and Marx 1965; Qi et al. 2026). In China, *C. pavimentata* was previously reported to have a wide distribution in Fujian, Guangdong, Guangxi, Guizhou, Hainan, Sichuan, Taiwan, Yunnan, and Zhejiang (e.g., Wu et al. 1985; Zhao et al. 1998; Zhao 2006). Recent taxonomic research, integrating morphological comparisons and mitochondrial DNA data, has shown that several populations in China previously assigned to *C. pavimentata* may actually represent misidentifications of recently described species such as *C. arcana*, *C. similis*, or *C. synergis* (Zhang et al. 2025a, 2025b; Qi et al. 2026). These findings suggest that the traditional concept of *C. pavimentata* in China and other recorded areas likely includes multiple cryptic or morphologically similar species (e.g. Korolev et al. 2026; Lalremsanga et al. 2026).

During recent fieldwork in Chongzuo and Guilin cities, Guangxi Zhuang Autonomous Region, China (see Fig. 1), we collected two unidentified snake specimens that were tentatively assigned to the genus *Calamaria* based on the following diagnostic characters: a cylindrical, vermiform body; a short, thick tail; indistinct demarcation between head and neck; small eyes with round pupils; reduced head scalation lacking internasals, loreals, and temporals; four or five supralabials, with the posterior supralabial broadly contacting the parietal; a large paraparietal scale; smooth dorsal scales arranged in 13 rows; a single cloacal plate; and paired subcaudal scales (Inger and Marx 1965; David et al. 2023). Based on the scalation and the morphology of the tail tip, these specimens were initially identified as *Calamaria* cf. *pavimentata*. However, subsequent detailed morphological examination revealed a suite of characters that clearly distinguish them from all described species of *Calamaria*. In particular, they differ markedly from members of the *C. pavimentata* species complex, including the nearly sympatric species *C. jinggangensis* and *C. similis*. Further molecular analyses of mitochondrial DNA (mtDNA) sequences, in combination with detailed morphological comparisons, demonstrated that these two specimens are significantly distinct from *C. pavimentata* from Java Island, Indonesia, *C. jinggangensis*, *C. similis*, and other congeners. Based on these lines of evidence, we conclude that the specimens represent a previously undescribed species of *Calamaria*. Accordingly, we herein formally describe these specimens as a new species within the genus *Calamaria*.

Materials and methods

Specimen collection and examination

We collected two specimens of *Calamaria* from Ningming County, Chongzuo City, and Lingui District, Guilin City, Guangxi Zhuang Autonomous Region, China. Following capture, the specimens were euthanized with tricaine methanesulfonate (MS-222), fixed in 4% formalin, and finally preserved in 75% ethanol at approximately 25 °C for morphological examination. The liver or muscle tissues were excised prior to fixation and stored in 95% ethanol at -40 °C as tissue samples for molecular experiments. Specimens were deposited in the herpetological collections of the Museum of Biology, Sun Yat-sen University (SYS), Guangdong, China and Guangdong Polytechnic of Environmental Protection Engineering, Foshan, Guangdong, China (GEP).

Molecular analyses

Total genomic DNA was extracted from liver tissue sample using the TIANamp Genomic DNA Kit (Tiangen Biotech Co., Ltd, Beijing). A fragment of the mitochondrial cytochrome b (cyt *b*) gene was amplified using the primer pair L14910 (5'–GACCT-GTGATMT-GAAAACCAYCGTTGT-3') and H16064 (5'–CTTTG-GTTTACAA-GAACAATGCTTTA-3') following Burbrink et al. (2000). PCR amplification was run using the following cycling conditions: initial denaturing step at 94 °C for 5 min; followed by 35 cycles of 94 °C for 30 s, 48 °C for 1 min and 72 °C for 70 s; and final extension step at 72 °C for 10 min. PCR products were purified with spin columns and then sequenced with forward primers using BigDye Terminator Cycle Sequencing Kit as per the guidelines on an ABI Prism 3730 automated DNA sequencer by Guangzhou Tianyi Huiyuan Bio-tech Co., Ltd.

Figure 1. Geographic distribution of *Calamaria incredibilis* sp. nov. and related species in Guangxi, China. White numbers indicate collecting localities: 1. Nazhi Village, Aidian Town, Ningming County, Chongzuo City; 2. Nonggang National NR, Longzhou County, Chongzuo City; 3. Shangjin Village, Shuikou Town, Longzhou County, Chongzuo City; 4. Luoxiang Town, Jinxiu County, Laibin City; 5. Huaping National Nature Reserve, Lingui District, Guilin City; 6. Huangsha Town, Longsheng County, Guilin City; 7. Caiwan Town, Quanzhou County, Guilin City. Source: 1 and 5 = This study; 2 and 3 = Qi et al. (2026); 4 = Fan (1931); 6 and 7 = Liang et al. (2024b).

The dataset of calamariid snakes comprises the sequences of the cyt *b* gene of two specimens of *Calamaria* sp. from Guangxi, China (SYS r02596 and GEP r093), along with 50 congeneric sequences (including representatives of 17 nominal *Calamaria* species) and three outgroups (following Korolev et al. 2026), including *Orientocoluber spinalis* (Peters), *Elaphe quatuorlineata* (Lacépède), and *Lycodon rufozonatus* (Cantor), which were obtained from the NCBI database Genbank (see Table 1). We initially aligned nucleotide sequences in MAFFT online (Katoh et al. 2019) with default parameters and subsequently checked them by eye in BioEdit 7.0.5.2 (Hall 1999) and adjusted when required. Protein-coding sequences were translated into amino acids to confirm that no pseudogenes had been amplified. The mean uncorrected genetic *p*-distances between cyt *b* sequences of *Calamaria* were calculated with MEGA 6.0 with the pairwise deletion option (Tamura et al. 2013). The best-fit substitution models for the data set were selected for genes and codon positions using Partitionfinder 2.1.1 (Lanfear et al. 2016) based on the Akaike information criterion (AIC), which selected GTR+I+G for the first codon position, HKY+I for the second codon position, and GTR+G for the third codon position of the cyt *b* gene.

We inferred the matrilineal genealogy of *Calamaria* using Bayesian inference (BI) and maximum likelihood (ML) approaches. We used the IQ-TREE (Nguyen et al. 2015) online server (Trifinopoulos et al. 2016) to generate the ML tree and assessed the confidence in tree topology using 1,000 ultrafast-bootstrap replications (UFBS; Minh et al. 2013). We conducted BI in the terminal version of MrBayes 3.1.2 (Huelsenbeck and Ronquist 2001; Ronquist et al. 2012). Both ML and BI trees used the same substitution models inferred from PartitionFinder. Metropolis-coupled Markov chain Monte Carlo (MCMCMC) analyses were run for the BI analysis with one cold chain and three heated chains for 10 million generations and sampled every 1,000 generations. The run was checked to ensure the effective sample sizes (ESS) were all above 200 by exploring the likelihood plots using TRACER v. 1.7 (Rambaut et al. 2018). We discarded the initial 1,000 trees as burn-in. We assessed the confidence in tree topology by the posterior probability (PP) of the nodes (Huelsenbeck and Ronquist 2001). We a priori regard nodes with UFBS values of 95% or higher and PP values over 0.95 as strongly supported; UFBS values between 95% and 90% and PP values between 0.95 and 0.90 were regarded as well-supported, and lower values were regarded as a lack of node support (Minh et al. 2013).

Table 1. DNA sequences, voucher specimens, and GenBank accession numbers of *Calamaria* and outgroup taxa used in this study.

No.	Species	Specimen voucher	Locality	cyt *b*	Sources
1	*C. incredibilis* **sp. nov.**	SYS r002596	Nazhi, Aidian, Ningming, Guangxi, China	PZ233954	This study
2	*C. incredibilis* **sp. nov.**	GEP r093	Huaping NR, Guilin, Guangxi, China	PZ233955	This study
3	*C. alcalai*	PNM 9873	Sitio Palbong, Barangay Batong Buhay, Sablayan, Mindoro, Philippines	MT819383	Weinell et al. 2021
4	*C. andersoni*	SYS r001699	Yingjiang, Yunnan, China	MH445955	Yang and Zheng 2018
5	*C. andersoni*	HS R20101	Dehong, Yunnan, China	OQ354844	Cai et al. 2023
6	*C. andersoni*	HS R20181	Tengchong, Yunnan, China	OQ354845	Cai et al. 2023
7	*C. annamensis*	VRTC NAP-17841	Bac Huong Hoa NR, Quang Tri, Vietnam	PX607279	Korolev et al. 2026
8	*C. annamensis*	VRTC NAP-17842	Bac Huong Hoa NR, Quang Tri, Vietnam	PX607280	Korolev et al. 2026
9	*C. annamensis*	VRTC NAP-17843	Bac Huong Hoa NR, Quang Tri, Vietnam	PX607281	Korolev et al. 2026
10	*C. arcana*	KFBG 14611	Mt. Dadongshan, Guangdong, China	ON482335	Yeung et al. 2022
11	*C. arcana*	HS 17082	Mt. Dawu, Guangdong, China	OQ354835	Cai et al. 2023
12	*C. arcana*	GP 9975	Yongxing, Hunan, China	OP980549	Cai et al. 2023
13	*C. arcana*	DL R199	Mt. Wuyi, Fujian, China	OQ354834	Cai et al. 2023
14	*C. berezowskii*	GXNU DLR194	Mt. Gongga, Sichuan, China	PP747047	Liang et al. 2024a
15	*C. berezowskii*	GXNU DLR195	Mt. Gongga, Sichuan, China	PP747048	Liang et al. 2024a
16	*C. berezowskii*	GXNU 20221215002	Mt. Gongga, Sichuan, China	PP747049	Liang et al. 2024a
17	*C. gervaisii*	KU 324661	Puguis, La Trinidad, Benguet, Luzon, Philippines	MT819384	Weinell et al. 2021
18	*C. gervaisii*	KU 334485	Narvacan, Ilocos Sur, Luzon, Philippines	MT819385	Weinell et al. 2021
19	*C. jinggangensis*	DL 20200725	Mt. Jinggangshan, Jiangxi, China	OQ354830	Cai et al. 2023
20	*C. jinggangensis*	DL 20200625-2	Mt. Jinggangshan, Jiangxi, China	OQ354831	Cai et al. 2023
21	*C. jinggangensis*	DL 20200625-3	Mt. Jinggangshan, Jiangxi, China	OQ354832	Cai et al. 2023
22	*C. jinggangensis*	DL 20200625-4	Mt. Jinggangshan, Jiangxi, China	OQ354833	Cai et al. 2023
23	*C. lumbricoidea*	KU 315159	Pasonanca NP, Zamboanga, Philippines	MT819388	Weinell et al. 2021
24	*C. lumbricoidea*	KU 334479	Mt. Lumot, Gingoog, Misamis, Philippines	MT819389	Weinell et al. 2021
25	*C.* cf. *lumbricoidea*	USMHC 1560	Air Itam Dam, Penang, Malaysia	MN338526	Quah et al. 2020
26	*C. mizoramensis*	MZMU 3141	Reiek, Mizoram, India	PX557820	Lalremsanga et al. 2026
27	*C. mizoramensis*	MZMU 3143	Reiek, Mizoram, India	PX557819	Lalremsanga et al. 2026
28	*C. mizoramensis*	MZMU 3144	Reiek, Mizoram, India	PX557818	Lalremsanga et al. 2026
29	*C. muelleri*	TNHC 58955	Gowa, South Sulawesi, Indonesia	MT819390	Weinell et al. 2021
30	*C. muelleri*	RMB 1283	Gowa, South Sulawesi, Indonesia	MT819391	Weinell et al. 2021
31	*C. nebulosa*	FMNH 258666	Phongsaly, Laos	MN338524	Quah et al. 2020
32	*C. palavanensis*	KU 309445	Barangay Irawan, Puerto Princessa, Palawan, Philippines	MT819386	Weinell et al. 2021
33	*C. palavanensis*	KU 311411	Mt. Mantalingahan, Rizal, Palawan, Philippines	MT819387	Weinell et al. 2021
34	*C. schlegeli*	LSUHC 10278	Bukit Larut, Perak, Malaysia	MN338525	Quah et al. 2020
35	*C. septentrionalis*	FTB 2839	unknown locality	KR814699	Pyron unpublished data
36	*C. septentrionalis*	KFBG 14506	Hainan, China	MH445956	Yang and Zheng 2018
37	*C. septentrionalis*	HS 11119 (CHS 116)	Tunxi, Huangshan, Anhui, China	MK201273	Li et al. 2020
38	*C. septentrionalis*	HS 12055 (CHS 118)	Huangshan, Anhui, China	MK201274	Li et al. 2020
39	*C. septentrionalis*	RE 30 (CHS 302)	Mangshan, Hunan, China	MK201384	Li et al. 2020
40	*C. septentrionalis*	SYS r000932 (CHS 613)	Mt. Tianjing, Guangdong, China	MK201434	Li et al. 2020
41	*C. septentrionalis*	HS R19100	Mt. Huangshan, Anhui, China	OQ354842	Cai et al. 2023
42	*C. septentrionalis*	HS 11145	Mt. Nanling, Guangdong, China	OQ354840	Cai et al. 2023
43	*C. septentrionalis*	DL 2021610-1	Huangsha, Guangxi, China	OQ354838	Cai et al. 2023
44	*C.* cf. *septentrionalis*	ROM 35605	Phia Oac-Phia Den NP, Cao Bang, Vietnam	AF471081	Lawson et al. 2005
45	*C.* cf. *septentrionalis*	ROM 35597	Phia Oac-Phia Den NP, Cao Bang, Vietnam	KX694890	Alencar et al. 2016
46	*C. similis*	KFBG 14507	Longzhou, Chongzuo, Guangxi, China	MH445957	Yang and Zheng 2018
47	*C. similis*	SYS r001816	Yangchun, Yangjiang, Guangdong, China	PZ158843	Qi et al. 2026
48	*C. similis*	SYS r001725	Nonggang NR, Guangxi, China	PZ158841	Qi et al. 2026
49	*C. similis*	SYS r001726	Nonggang NR, Guangxi, China	PZ158842	Qi et al. 2026
50	*C. synergis*	AHNU ZR24046	Mt. Jinuo, Xishuangbanna, Yunnan, China	PV745121	Zhang et al. 2025a
51	*C. yunnanensis*	ROM 41547	Simao, Yunnan, China	KX694891	Zaher et al. 2009
52	*C. yunnanensis*	YPX 503	Yunnan, China	JQ598922	Grazziotin et al. 2012
	Outgroups				
53	*Orientocoluber spinalis*	MVZ 211019	Ningxia, China	AY486924	Nagy et al. 2004
54	*Elaphe quatuorlineata*	LSUMZ 40626	Hungary	AY486931	Nagy et al. 2004
55	*Lycodon rufozonatus*	LSUMZ 44977	China	AF471063	Lawson et al. 2005

Morphological analysis

Terminology and measurements follow Inger and Marx (1965) and Poyarkov et al. (2019). Measurements were taken with a digital slide calliper to the nearest 0.1 mm, except for body and tail lengths, which were measured to the nearest millimeter with a measuring tape. The number of ventral scales was counted according to Dowling (1951). The numbers of dorsal scale rows are given at one head length behind the head, at midbody, and at one head length before the vent. The sex was determined by dissection (inspection of gonads) and/or by tail shape when dissection was not possible. Maxillary teeth of the specimens were counted by examining both maxillae using a dissecting pin under a binocular microscope prior to preservation.

The following measurements (all in mm) and counts were taken: snout-vent length (SVL); tail length (TaL); total length (TL); ratio of tail length/total length (TaL/TL); anterior dorsal scale rows (ASR); dorsal scale rows at midbody (MSR); posterior dorsal scale rows (PSR); supralabial scales (SL); number of supralabials touching the eye (SLE); infralabial scales (IL); preocular scales (PrO); postocular scales (PoO); subcaudal scales (SC); ventral scales (VEN). Asymmetric characters are given in left/right order.

Morphological characters of the examined specimens were compared in detail with those of other *Calamaria* species known from mainland China and the Indo-Burma Region. For comparative purposes, we relied on previously published data (e.g., Duméril et al. 1854; Inger and Marx 1965; Darevsky and Orlov 1992; Ziegler and Le 2005; Ziegler et al. 2007, 2008, 2019; Orlov 2009; Orlov et al. 2010; Yang and Zheng 2018; Poyarkov et al. 2019; Lee 2021; Yeung et al. 2022; Cai et al. 2023; Liang et al. 2024a; Nguyen et al. 2025; Zhang et al. 2025a, 2025b; Bharali et al. 2026; Korolev et al. 2026; Lalremsanga et al. 2026; Qi et al. 2026). Other abbreviations: **Mt.** = Mountain; **NR** = Nature Reserve; **NP** = National Park; **asl** = above sea level; **ZAR** = Zhuang Autonomous Region.

Osteological examination

To study the skeletal morphology of *Calamaria*, we performed detailed micro-CT scanning for a single specimen, SYS r002596. The X-ray scanning was carried out with Nano-computerized tomography. Specimens were scanned using a GE v|tome|x m dual tube 300/180kV system in the Key Laboratory of Vertebrate Evolution and Human Origins, Institute of Vertebrate Paleontology and Paleoanthropology (IVPP), Chinese Academy of Sciences, China. The specimen was scanned with an energy beam of 80 kV and a flux of 80 μA using a 360° rotation and then reconstructed into the 4096*4096 matrix of 1536 slices. The final CT reconstructed skull images were exported with a minimum resolution of 4.137 μm. The skull images were exported from the virtual 3D model which was reconstructed by Volume Graphics Studio 3.0.

Results

Sequence variation

The final alignment of the cyt *b* mtDNA gene fragment contained 1,109 aligned nucleotides, of which 554 sites were conserved, 555 sites were variable, and 481 were parsimony-informative. The transition-transversion bias (R) was estimated at 5.01. Nucleotide frequencies were 31.74% (A), 28.47% (T), 29.05% (C), and 10.74% (G) (all data are given for the ingroup only). We deposited the newly obtained sequences in GenBank (see Table 1).

Phylogenetic relationships

The obtained matrilineal mtDNA-based genealogy agrees with the phylogenetic reconstructions presented in several recent publications on *Calamaria* taxonomy (Korolev et al. 2026; Lalremsanga et al. 2026; Qi et al. 2026) in recognizing three major clades within the genus: Clade A (Sundaland species), Clade B (Northeast India), and Clade C (Indochina, China and East Asian islands) (Fig. 2). ML and BI analyses yielded largely congruent topologies, with minor differences restricted to deeper nodes within Clade A, which are not relevant to the present study (Fig. 2). The genus *Calamaria* was strongly supported as monophyletic (100/1.0; node support values hereafter given as ML UFBS/BI PP, respectively), with all sampled species grouped into three well-supported major clades.

Phylogenetic relationships among species within Clades A (100/1.0) and B (100/1.0) were reconstructed the same way as described in Lalremsanga et al. (2026), Korolev et al. (2026) and Qi et al. (2026). As these species are not important for the goal of the present manuscript, we will not describe their phylogenetic relationships in detail and focus on topology recovered within the Clade C (100/1.0), which comprises species distributed in Indochina and East Asia. *Calamaria nebulosa* and *C. annamensis* occupy the basal position in Clade C, with the former recovered as sister to all remaining members of this clade, though with small nodal support (82/0.90). The remaining species of Clade C form a well-supported group (94/0.99), and is further subdivided into three subgroups. The first subgroup (98/1.0, strong support) includes *C. arcana*, *C. jinggangensis*, and *C. septentrionalis*, with strongly supported sister relationships between *C. arcana* and *C. jinggangensis* (100/1.0). Within the *C. septentrionalis* complex, the Vietnamese samples of *C.* cf. *septentrionalis* from Cao Bang Province (ROM 35605, ROM 35597) form a lineage sister to Chinese populations of nominative *C. septentrionalis* (100/1.0). The second subgroup (81/0.90, moderate support) includes sister species *Calamaria berezowskii* from Sichuan Province, China, and *C. similis* from Guangdong Province and Guangxi ZAR, China. Importantly, the third group (76/0.90, moderate support) includes the two

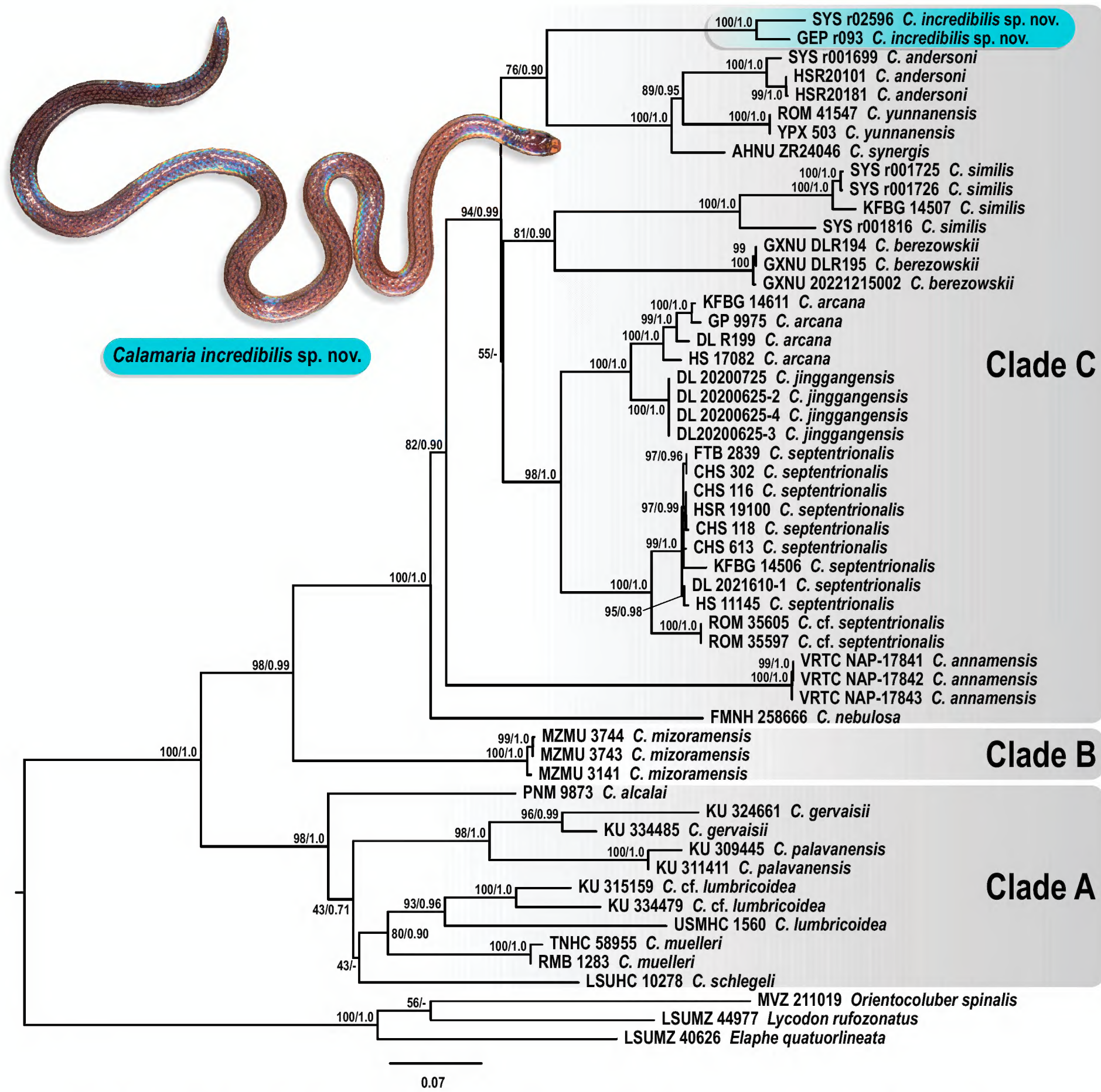

Figure 2. Maximum Likelihood (ML) phylogenetic tree of *Calamaria* derived from the analysis of 1,109 bp of cyt *b* mitochondrial gene fragment. For voucher specimen information and GenBank accession numbers see Table 1. Values at the nodes correspond to ML UFBS/BI PP support values.

specimens of *Calamaria* sp. from Chongzuo and Guilin cities, Guangxi ZAR, China (which form a strongly supported group; 100/1.0), together with *C. yunnanensis*, *C. andersoni*, and *C. synergis* (100/1.0). Within the latter group, *C. yunnanensis* is sister to *C. andersoni* (89/0.95), whereas *C. synergis* is sister to that pair.

Genetic distances

The uncorrected *p*-distances for the cyt *b* gene fragment among the *Calamaria* species examined are shown in Table 2. Pairwise interspecific distances ranged from 6.29% (between *C. jinggangensis* and *C. arcana*) to 24.95% (between *C. berezowskii* and *C. schlegeli*). The *Calamaria* sp. lineage is recovered as sister to a well-supported clade comprising *C. yunnanensis*, *C. andersoni*, and *C. synergis*. It differs from these three species by substantial mitochondrial divergence in the cyt *b* gene, with uncorrected *p*-distances of 14.97% from *C. yunnanensis*, 14.52% from *C. andersoni*, and 12.72% from *C. synergis*. Genetic divergence between *Calamaria* sp. and other congeners ranged from 18.46% (*C. berezowskii*) to 20.96% (*C. lumbricoidea*). Intraspecific divergence between the two samples of *C. incredibilis* sp. nov. from Chongzuo and Guilin cities, Guangxi ZAR, was moderate (4.19%). Comparable or higher intraspecific divergence values were observed in several other Calamaria species, including *C. gervaisii* (8.87%) and *C.* cf. *lumbricoidea* (7.48%) (Table 2).

Table 2. Uncorrected *p*-distances (percentage) between *Calamaria* species based on 1,109 base pairs from the mitochondrial cyt *b* gene. Notes: n/a = Not available.

	Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	*C. incredibilis* sp. nov.	**4.19**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	*C. alcalai*	18.14	**n/a**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	*C. andersoni*	14.52	20.73	**1.20**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	*C. annamensis*	17.42	20.73	17.86	**0.20**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	*C. arcana*	14.75	20.27	18.34	17.34	**2.94**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	*C. berezowskii*	18.46	23.68	18.96	17.66	17.71	**0.20**	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	*C. gervaisii*	18.52	15.38	19.91	20.72	18.75	22.33	**8.87**	0	0	0	0	0	0	0	0	0	0	0	0	0
8	*C. jinggangensis*	12.87	19.21	16.17	18.16	6.29	18.46	15.87	**0.00**	0	0	0	0	0	0	0	0	0	0	0	0
9	*C. palavanensis*	17.72	14.64	19.6	19.39	20.42	22.03	13.09	17.48	**2.38**	0	0	0	0	0	0	0	0	0	0	0
10	*C. lumbricoidea*	20.96	18.29	21.96	21.46	20.96	22.06	19.05	20.66	16.09	**n/a**	0	0	0	0	0	0	0	0	0	0
11	*C.* cf. *lumbricoidea*	20.76	15.57	22.43	21.66	20.41	22.85	17.49	18.92	15.84	15.57	**7.48**	0	0	0	0	0	0	0	0	0
12	*C. mizoramensis*	18.41	15.85	19.26	20.86	16.84	23.25	15.87	15.27	17.17	18.86	19.69	**0.00**	0	0	0	0	0	0	0	0
13	*C. muelleri*	17.58	14.9	21.46	20.53	17.81	21.05	15.09	16.49	15.94	15.86	13.32	17.42	**0.63**	0	0	0	0	0	0	0
14	*C. nebulosa*	14.07	18.29	15.57	16.67	17.37	15.67	19.04	17.07	18.28	18.56	20	20.96	18.98	**n/a**	0	0	0	0	0	0
15	*C. schlegeli*	20.51	16.77	22.65	20.66	20.51	24.95	16.02	19.76	15.91	19.16	17.24	18.26	16.18	17.66	**n/a**	0	0	0	0	0
16	*C. septentrionalis*	12.67	21.07	14.01	17.4	11.35	18.00	18.95	9.85	18.24	21.22	20.88	17.86	20.32	18.33	22.55	**0.50**	0	0	0	0
17	*C.* cf. *septentrionalis*	12.72	22.56	14.77	17.27	10.18	16.37	19.66	10.78	19.06	20.66	20.93	19.76	21.15	16.77	22.16	4.03	**0.00**	0	0	0
18	*C. similis*	17.74	22.64	19.51	19.06	18.32	17.61	20.87	17.22	20.22	21.78	23.38	20.06	22.47	17.89	21.86	16.6	17.74	**5.79**	0	0
19	*C. synergis*	12.72	18.9	8.08	16.97	14.37	18.06	19.2	12.28	18.6	20.36	19.22	17.66	19.29	14.37	19.46	12.71	12.87	17.44	**n/a**	0
20	*C. yunnanensis*	14.97	21.95	11.38	19.66	18.19	18.66	22.38	15.87	21.79	20.96	20.45	21.56	23.33	15.87	23.35	15.34	14.37	19.91	7.78	**0.00**

Taxonomic conclusion

Based on combined evidence from detailed morphological comparisons and mitochondrial DNA analyses, the *Calamaria* population from Chongzuo and Guilin cities, Guangxi ZAR, China is closely allied to members of the *Calamaria pavimentata* species complex, including sympatric species such as *C. jinggangensis* and *C. similis*, and is here regarded as representing an independent evolutionary lineage. We therefore describe this population as a new species.

Calamaria incredibilis sp. nov.

https://zoobank.org/8B9E730D-5AF6-44A4-A074-B75C25025D93

Tables 3, 4, Figs 3–6

Type material. ***Holotype.*** • SYS r002596, adult male, from Nazhi Village (那支村), Aidian Town, Ningming County, Chongzuo City, Guangxi ZAR, China (21.8597°N, 107.0169°E; altitude 1060 m asl), collected by Shuo Qi on 25 April 2021.

Paratype (n = 1) • GEP r093, adult male from Huaping National NR (花坪国家级自然保护区), Lingui District, Guilin City, Guangxi ZAR, China (25.6270°N, 109.9137°E; altitude 760 m asl), collected by Jian Wang, Zhao-Chi Zeng, and Hong-Hui Chen on 23 April 2025.

Diagnosis. *Calamaria incredibilis* sp. nov. can be distinguished from all other congeners by the combination of the following morphological characters: nine enlarged maxillary teeth; rostral higher than wide; prefrontal shorter than frontal and contacting the first two supralabials; mental not in contact with anterior chin shields; dorsal scales in 13–13–13 rows, smooth throughout; a single preocular and postocular; four supralabials, with the 2nd and 3rd ones contacting the eye; five infralabials; six scales surrounding the paraparietal; 170–182 ventrals in males; 21–23 paired subcaudals in males; a relatively short tail (8.2–8.4% of total length in males), thick and nearly cylindrical, gradually tapering to an obtuse point; dorsal coloration brown, seven longitudinal series of interrupted dark brown stripes are visible along the body, extending from behind the collar to the tip of the tail; the margins of the dorsal scales are heavily suffused with black pigment, forming an almost reticulate pattern; the ventral surface yellowish white, with dark brown blotches along the outermost lateral margins; absence of light spots on the dorsal tail.

Description of the holotype. SYS r002596, adult male (see Fig. 3); specimen in good condition, slightly discolored due to preservation. Body slender, cylindrical (SVL 222.7 mm); tail short, slightly thinner than body, thick and nearly cylindrical, gradually tapering to an obtuse point (TaL 20.4 mm, TaL/TL 8.4%). Head small, elliptical in dorsal view (head length 7.3 mm; head width 4.2 mm; head height 3.0 mm). Eye small, round (eye diameter 0.8 mm), eye-nostril distance 1.5 mm, eye-mouth distance 0.7 mm.

Head scalation. Rostral broader than high (rostral width 1.8 mm, rostral height 1.2 mm); dorsal portion visible from above approximately half the length of the prefrontal suture. Prefrontal shorter than frontal, not entering orbit, in contact with the first and second supralabials. Frontal hexagonal, longer than wide (frontal length 2.5 mm, frontal width 1.6 mm). Temporals absent. Paraparietal surrounded by six scales. One preocular on each side, higher than wide, slightly taller than postocular but shorter than eye diameter. One postocular on each side, also higher than wide. Nasals divided, small, bordered by rostral, prefrontal, and 1st supralabial. Four supralabials on each side, the 2nd and 3rd entering the orbit; the 4th is markedly larger than the other three (relative size: 4 > 2 > 3 > 1). Five infralabials on each side, the first three pairs contacting anterior chin shields; the 1st pair meeting at the midline; the 3rd largest. Anterior chin shields much longer than wide, pentagonal, meeting at the midline. Posterior chin shields are longer, in contact anteriorly, and separated posteriorly by first gulars. Mental triangular, not in contact with anterior chin shields.

Body scalation. Dorsal scale rows 13–13–13 throughout body, all smooth. Ventrals 170 (+ 3 gulars); subcaudals 21, all paired. Cloacal plate undivided.

Coloration of the holotype. In life, the dorsal surface of head is brown, with blackish pigment forming a mask-like marking dorsally; the lateral surfaces of the head are slightly paler than the dorsum, with blackish pigment forming a longitudinal mask extending from the rostral

Table 3. Selected measurements and meristic characters of *Calamaria incredibilis* sp. nov. and *Calamaria* cf. *pavimentata* in Guangxi ZAR and Guizhou Province, China. Notes: H = holotype; P = paratype; M = adult male; F = adult female; * = damaged specimen; n/a = not available.

Voucher	Locality	Sex	SVL (mm)	TaL (mm)	ASR-MSR-PSR	VEN	Anal	SC	SL	SL-E	IL	PrO	PoO	Sources
***Calamaria incredibilis* sp. nov.**														
SYS r002596[H]	Nazhi, Aidian, Ningming, Guangxi	M	222.7	20.4	13-13-13	170	1	21	4/4	2-3/2-3	5/5	1/1	1/1	3
GEP r093[P]	Huaping NR, Guilin, Guangxi	M	209.5	18.6	13-13-13	182	1	23	4/4	2-3/2-3	5/5	1/1	1/1	3
Calamaria* cf. *pavimentata														
No. 1016*	Jinxiu, Laibin, Guangxi	M	180	14	13-13-13	179	1	22	4/4	2-3/2-3	5/5	1/1	1/1	1
No. 2009*	Jinxiu, Laibin, Guangxi	F	273	13	13-13-13	n/a	n/a	n/a	4/4	2-3/2-3	5/5	1/1	1/1	1
770525	Wangmo, Qianxinan, Guizhou	M	146	16	13-13-13	181	1	23	4/4	2-3/2-3	5/5	1/1	1/1	2
770596	Wangmo, Qianxinan, Guizhou	M	233	17	13-13-13	188	1	21	4/4	2-3/2-3	5/5	1/1	1/1	2
770597	Wangmo, Qianxinan, Guizhou	M	213	17	13-13-13	181	1	21	4/4	2-3/2-3	5/5	1/1	1/1	2

Source: 1 = Fan (1931); 2 = Wu et al. (1985); 3 = This study.

region to the temporal region. The ventral surface of the head is yellowish white, with irregular dark brown blotches. The dorsal surface of the body is brown. Two nuchal collars are present, the first is a distinct dark brown collar, slightly shorter than the head length and extending laterally onto the sides of the neck; the second is smaller, pale, pattern-less, and approximately one to two dorsal scales in length. Seven longitudinal series of interrupted dark brown stripes are visible along the body, extending from behind the pale-colored collar to the tip of the tail. The margins of the dorsal scales are heavily suffused with black pigment, forming an almost reticulate pattern. The ventrals are pale yellow, with dark brown blotches along the outermost lateral margins, forming a dashed line parallel to the longitudinal stripes. The tail dorsum is slightly darker than the body dorsum, and the longitudinal stripes fade posteriorly. Light spots are absent on the dorsal tail. Subcaudal surface pale yellow, generally immaculate with only a few scattered dark pigment blotches.

In preservative, the head, body, and tail dorsum fade to dark brown. Two nuchal collars remain in strong contrast. The dark brown longitudinal stripes become much more diffuse, whereas the reticulate pattern formed by the heavily pigmented margins of the dorsal scales becomes more conspicuous. The ventral surfaces of the head, body, and tail are generally pale white, only with tiny dark speckles on the ventral surfaces of tail.

Skull morphology of holotype (Fig. 4). The skull is subcylindrical in general shape. In dorsal view, the anterior margin of the premaxilla is flat, the nasals and septomaxillae are relatively strong and laterally expanded, the conchal processes of the septomaxillae are broad, flattened, and well-developed. The frontals are approximately right-triangle-shaped with their anterior tip rounded. The parietal is scutiform, longer than wide. The supraoccipital, preoccipital, and exoccipitals are fully fused into a complex that forms the widest part of the braincase.

In ventral view, the vomers are well-developed with their anterior tips nearly reaching the vomerine processes of premaxilla. The maxillary processes of palatines are triangular and laterally expanded while the choanal processes. The pterygoid is slender and lanceolate in shape, twice the length of the palatine. The basisphenoid and basioccipital lack a ventral process. The parasphenoid rostrum of the basisphenoid is sharp and triangular-shaped. The basioccipital is relatively flat and laterally expanded.

In lateral view, the ascending process of premaxilla is slender and greatly reduced. The conchal process of the

Table 4. Comparison of morphological characters of *Calamaria incredibilis* sp. nov. with those of congeners occurring in China and the Indo-Burma region. Symbols: (1) = Supralabials; (2) = Supralabials contacting orbit; (3) = Preocular (1 = present, 0 = absent); (4) = Mental touching chin shields (1 = yes, 0 = no); (5) = Number of scales contacting paraparietal; (6) = VEN in males; (7) = VEN in females; (8) = SC in males; (9) = SC (females); (10) = maximum TL (mm) in males; (11) = maximum TL (mm) in females; (12) = ratio TaL/TL (%) in males; (13) = ratio TaL/TL (%) in females; (14) = Tail: tapering (2), slightly tapered (1), or not (0); (15) = End of tail; (16) = Dorsal color; (17) = Ventrals color. Notes: n/a = not available.

Species	1	2	3	4	5	6	7	8	9	10	11	12
***C. incredibilis* sp. nov.**	4	2/3	1	0	6	170–182	n/a	21–23	n/a	243	n/a	8.2–8.4
C. abramovi	4	2/3	1	0	6	159	174	26	20	139	482	13.3
C. andersoni	4	2/3	1	0	6	164–172	186	20–23	14	351	312	8.8–9.2
C. annamensis	4	2/3	1	0	6	182	196–204	22	14–15	304	552	6.6
C. arcana	4	2/3	1	0	6	170–176	192	20–22	12	303	n/a	7.2–11.8
C. berezowskii	4	2/3	1	0	6	149–155	153–171	22–25	12–16	290	245	6.6–10.5
C. buchi	4	2/3	1	1	5	n/a	221–236	n/a	13–14	n/a	466	n/a
C. concolor	5	2/3	1	1	5	209	n/a	19	n/a	578	n/a	7.2
C. dominic	4 or 5	2/3 or 3/4	1	1 or 0	6	n/a	174	n/a	17 or 18	n/a	421	n/a
C. garoensis	4	2/3	1	0	6	165	185–187	27	12–16	225	278	14.2
C. gialaiensis	4	2/3	1	1	5	191	n/a	23	n/a	457	n/a	8.1
C. jinggangensis	4	2/3	1	0	6	157–158	179	20	12	260	364	15
C. lovii ingermarxorum	4	2/3	0	1	6	205	n/a	23	n/a	318	n/a	7.4
C. lumbricoidea	5	3/4	1	1	4 or 5	144–196	137–229	17–27	13–21	498	642	6.3–11.4
C. mizoramensis	4	2/3	1	0	6	147–155	166–175	22–27	13–15	251	258	10.3–13.1
C. nebulosa	4	2/3	0	0	6	n/a	179	n/a	22	n/a	354	n/a
C. pavimentata	4	2/3	1	0	6	151	136	27	13	206	125	11.6
C. sangi	4	2/3	1	1	5 or 6	190	n/a	19	n/a	373	n/a	6.2
C. schlegeli	5	3/4	1 or 0	0	5 or 6	129–161	136–180	25–44	19–37	391	395	11.1–21.3
C. septentrionalis	4	2/3	1	0	6	148–166	168–188	15–19	6–11	344	384	6.3–8.6
C. similis	4	2/3	1	0	6	145–155	168	20–23	15	187	154	6.4–9.3
C. strigiventris	4	2/3	1	0	6	130–168	176–183	29–31	20–22	362	367	11.2–17.9
C. synergis	4	2/3	1	0	5	161–166	n/a	20–23	n/a	284	n/a	6.6–9.2
C. thanhi	4	2/3	0	0	6 or 7	184	198	28	21	461	455	9.9
C. yunnanensis	4	2/3	0	0	6	167–184	199	15–20	19	300	516	8.2–8.8

Table 4. Continued.

Species	13	14	15	16	17	Sources
***C. incredibilis* sp. nov.**	n/a	2	obtuse point	reddish brown to dark brown with narrow dark longitudinal stripes	yellowish white	This study
C. abramovi	7.1	2	sharp point	uniform black	yellow-orange spots	Orlov et al. 2009
C. andersoni	5.8	0	obtuse point	brownish with faint narrow black lateral stripes	orange-yellow, immaculate	Yang and Zheng 2018; Zhang et al. 2025b
C. annamensis	3.9–4.7	1	obtuse point	uniform dark brown to olive-brown	light orange to salmon with small black spots	Korolev et al. 2026
C. arcana	4.7	0	obtuse point	brownish	orangish-red, immaculate	Yeung et al. 2022; Zhang et al. 2023
C. berezowskii	6.5–6.9	0	obtuse point	blackish-brown or brown	light khaki or white	Inger and Marx 1965; Liang et al. 2024a
C. buchi	3.9–4.1	1	obtuse point	blackish with small light spots	yellow, immaculate	Inger and Marx 1965; Ziegler et al. 2009
C. concolor	n/a	1	obtuse point	uniform orangish-red	bright red, immaculate	Orlov et al. 2010; Nguyen et al. 2025
C. dominic	6.2	1	obtuse point	dark with irregular yellow blotches	dark with few yellow blotches & bands	Ziegler et al. 2019
C. garoensis	4.8–5.5	0	obtuse point	dark brown to blackish-brown with three to six narrow longitudinal stripes	yellow, immaculate	Bharali et al. 2026
C. gialaiensis	n/a	0	rounded	light grayish-brown with a faint dark neck collar and a few dark blotches along the posterior vertebral region	yellowish beige, immaculate	Ziegler et al. 2009
C. jinggangensis	3.6	0	obtuse point	brownish black	dark orange	Darevsky and Orlor 1992; Cai et al. 2023; Zhang et al. 2024
C. lovii ingermarxorum	n/a	0	blunt	immaculate bluish-gray with light spots on four lateral neck scales	dark gray, immaculate	
C. lumbricoidea	3.9–8.3	1	sharp point	black with narrow cream or yellow rings; head red or pink in juveniles	yellow with black ventral scales forming bands	Inger and Marx 1965
C. mizoramensis	4.7–6.5	0	obtuse point	dark brown to blackish-brown with three to six narrow longitudinal stripes	yellow, immaculate	Lalremsanga et al. 2026
C. nebulosa	7.9	0	obtuse point	bluish-gray	yellow, immaculate	Lee 2021
C. pavimentata	8	2	obtuse point	blackish-brown with narrow dark longitudinal stripes	yellowish white, immaculate	Duméril et al. 1854; This study
C. sangi	n/a	1	obtuse point	grayish-brown with fine dark mottling	cream with narrow dark transverse bands	Nguyen et al. 2009
C. schlegeli	7.3–14.4	0	blunt	immaculate gray or brown; head variably pink, yellow, and/or brown	cream, immaculate	Inger and Marx 1965
C. septentrionalis	2.6–4.3	0	broadly rounded	dark brown or black dorsally, usually with a narrow yellow ring about six to eight scales behind the head	yellow, with small black spots	Inger and Marx 1965
C. similis	6.1	2	obtuse point	reddish brown to dark brown with narrow dark longitudinal stripes	pale yellow	Qi et al. 2026
C. strigiventris	8.4–8.6	2	abruptly to point	uniform grey-brown	bright yellow with longitudinal black stripes	Poyarkov et al. 2019
C. synergis	n/a	0	obtuse point	blackish-brown	light khaki, immaculate	Zhang et al. 2025a
C. thanhi	6.8	2	gradually to a point	dark with 4–6 light body bands	yellow, immaculate	Ziegler et al. 2005, 2007
C. yunnanensis	5.4–8.2	2	obtuse point	blue-gray to olive-brown	orange-yellow, immaculate	Lee 2021; Zhang et al. 2025b

septomaxillae is anteroposteriorly expanded, reaching the lateral edge of nasals. The prefrontal and postorbital are similar in height, the bottom tip of the postorbital reaches the top margin of the maxilla. The ectopterygoid is biforked, the labial furcula of ectopterygoid is oval, and distinct from the lingual process. The lingual process projects anterodorsally, overlaps the dorsal margin ectopterygoid process of the maxilla, visible in lateral view but invisible in ventral view.

The mandible is slender and moderately curved. The prearticular crest of the compound bone is prominent while the surangular crest is absent.

Dentition of the holotype (Fig. 4). The maxillary teeth are laterally compressed, reduced in number, with their distal tip posteriorly recurved. The morphology of palatine teeth, pterygoid teeth, and dentary teeth show no significant specialization relative to the maxillary teeth. Maxillary teeth 9, palatine teeth 6, pterygoid teeth 10/11, dentary teeth 8 on each side.

Variation (Figs 5, 6). Variation in measurements and scalation of the type series is summarized in Table 3. The two specimens are generally similar in overall appearance. However, in the paratype, the posterior portion of the ventral surface is slightly darker, being pale yellow

Figure 3. *Calamaria incredibilis* sp. nov, adult male (SYS r002596, holotype) in preservative. **A.** Dorsal view of body; **B.** Ventral view of body; **C.** Dorsal view of head; **D.** Ventral view of head; **E.** Lateral view of head, right side; **F.** Dorsal view of tail (posterior body). Photographs by SQ.

compared to the yellowish white anterior portion. In addition, the ventral scales are scattered with more tiny dark speckles than in the holotype.

Etymology. The specific epithet *incredibilis* is a Latin adjective meaning "unbelievable" or "extraordinary," referring to the unexpectedly high level of cryptic diversity revealed by the discovery of this species, particularly in relation to closely allied taxa within the *C. pavimentata* species complex and their close geographic proximity. Based on the type locality, we propose the following common names: "Guangxi Reed Snake" (English), 广西两头蛇 (*guǎng xī liǎng tóu shé*, Chinese), "Rắn mai gầm quảng tây" (Vietnamese), and Гуансийская карликовая змея (*Guansiyskaya karlikovaya zmeya*, Russian).

Comparison. Comparative morphological data for *Calamaria incredibilis* sp. nov. and currently recognized members of the genus *Calamaria* from mainland China and the Indo-Burma Region are summarized in Table 4.

Calamaria incredibilis sp. nov. is readily distinguished from the nearly sympatric species *C. jinggangensis* and *C. similis* by a unique combination of morphological characters. It differs from *C. jinggangensis* by having more ventral scales in males (VEN 170–182 vs. 157–158); more subcaudal scales in males (SC 21–23 vs. 20); a markedly shorter relative tail length in males (TaL/TL 8.2–8.4% vs. 15.0%); a yellowish-white ventral surface (vs. dark orange); dark brown pigmentation along the lateral margins of the ventrals (vs. immaculate); and by

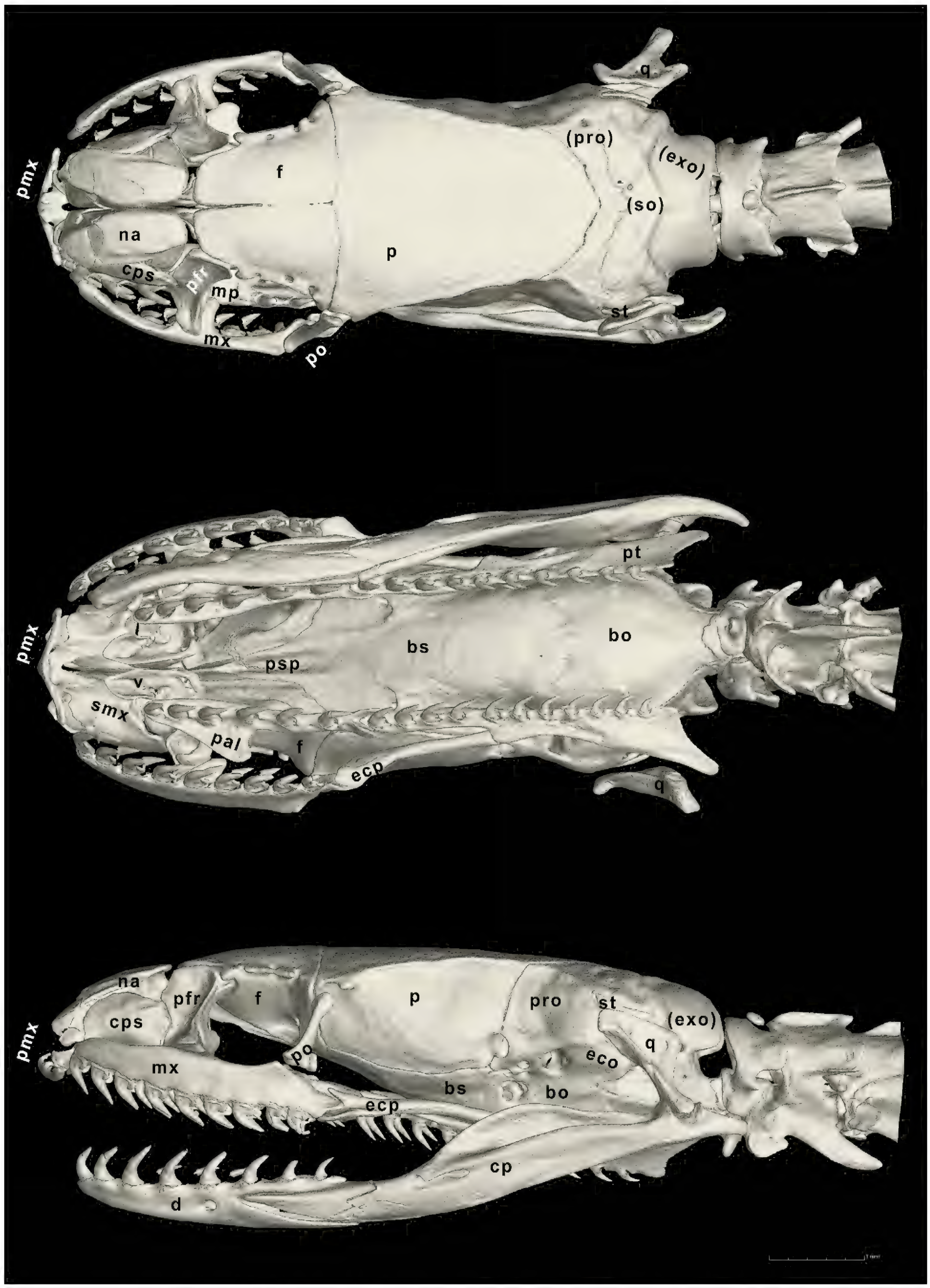

Figure 4. Three-dimensional model of the skull of *Calamaria incredibilis* sp. nov, adult male (SYS r002596, holotype). Top, dorsal view; middle, ventral view; bottom, lateral view. Abbreviations: bo, basioccipital; bs, basisphenoid; cps, conchal process of septomaxilla; ecp, ectopterygoid; exo, exoccipital; mp, maxillary process of palatine; mx, maxilla; na, nasal; p, parietal; pal, palatine; pfr, prefrontal; pmx, premaxilla; po, postorbital; pro, preoccipital; psp, parasphenoid rostrum; pt, pterygoid; q, quadrate; smx, septomaxilla; so, supraoccipital; st, supratemporal. Implemented by JSS.

Figure 5. *Calamaria incredibilis* sp. nov., adult male (GEP r093, paratype) in life. Photograph by JW.

the absence of a light blotch at the vent and two light blotches on each flank near the distal portion of the tail (vs. present). *Calamaria incredibilis* sp. nov. differs from *C. similis* by having more ventral scales in males (VEN 170–182 vs. 145–155); the absence of a light blotch at the vent and two light blotches on each flank near the distal portion of the tail (vs. present).

Moreover, *Calamaria incredibilis* sp. nov. differs from *C. pavimentata* sensu stricto (Java Island, Indonesia) by having more ventral scales in males (VEN 170–182 vs. 151); fewer subcaudal scales in males (SC 21–23 vs. 27); and a markedly shorter relative tail length in males (TaL/TL 8.2–8.4% vs. 11.6%). In addition, *Calamaria incredibilis* sp. nov. can be distinguished morphologically from the six junior synonyms or subspecies historically assigned to *C. pavimentata*. It differs from *Calamaria siamensis* by having a lower maximum number of ventral scales in males (VEN up to 182 vs. 190) and by the presence of a distinct pale nuchal collar (vs. absent or indistinct). It further differs from *Calamaria pavimentata* var. *uniformis* by having more ventral scale counts in males (VEN 170–182 vs. 143–149) and fewer subcaudal scales in males (SC 21–23 vs. 30–34). From *Calamaria pavimentata formosana*, the new species differs by having a markedly shorter relative tail length in males (TaL/TL 8.2–8.4% vs. 8.6–13.2%). It differs from *Calamaria pavimentata banaensis* by having more ventral scale counts in males (VEN 170–182 vs. 157–160) and by lacking a dark midventral stripe on the belly (vs. present). Finally, *Calamaria incredibilis* sp. nov. differs from *Calamaria pavimentata miyarai* by having a pale nuchal collar (vs. absent or indistinct).

Calamaria incredibilis sp. nov. is readily distinguished from *C. lumbricoidea* and *C. schlegeli* by having four supralabials, with the second and third in contact with the eye (vs. five supralabials, with the third and fourth in contact with the eye). Furthermore, both species are restricted to areas south of the Isthmus of Kra in Peninsular Malaysia and have not been recorded from mainland Indochina. *Calamaria incredibilis* sp. nov. also differs from *C. lovii ingermarxorum*, *C. nebulosa*, *C. thanhi* and *C. yunnanensis* by the presence of a preocular scale (vs. absent). It further differs from *C. buchi*, *C. concolor*, *C. gialaiensis*, *C. lovii ingermarxorum*, *C. lumbricoidea*, and *C. sang* in having the mental not contacting the chin shields (vs. contacting). In addition, *Calamaria incredibilis* sp. nov. differs from several other congeners distributed in mainland China and the Indo-Burma Region by having more ventral scales in males. Specifically, it can be distinguished from *C. abramovi* by having more ventral scales in males (VEN 170–182 vs. 159); from *C. berezowskii* (VEN 170–182 vs. 149–155); from *C. garoensis* (VEN 170–182 vs. 165); from *C. mizoramensis* (VEN 170–182 vs. 147–155); from *C. septentrionalis* (VEN 170–182 vs. 148–166); from *C. strigiventris* (VEN 170–182 vs. 130–168); and from *C. synergis* (VEN 170–182 vs. 161–166). Compared with *Calamaria andersoni*, *Calamaria incredibilis* sp. nov. has a tail gradually tapering posteriorly (vs. not tapering), yellowish-white ventral surfaces (vs. orange-yellow), and the presence

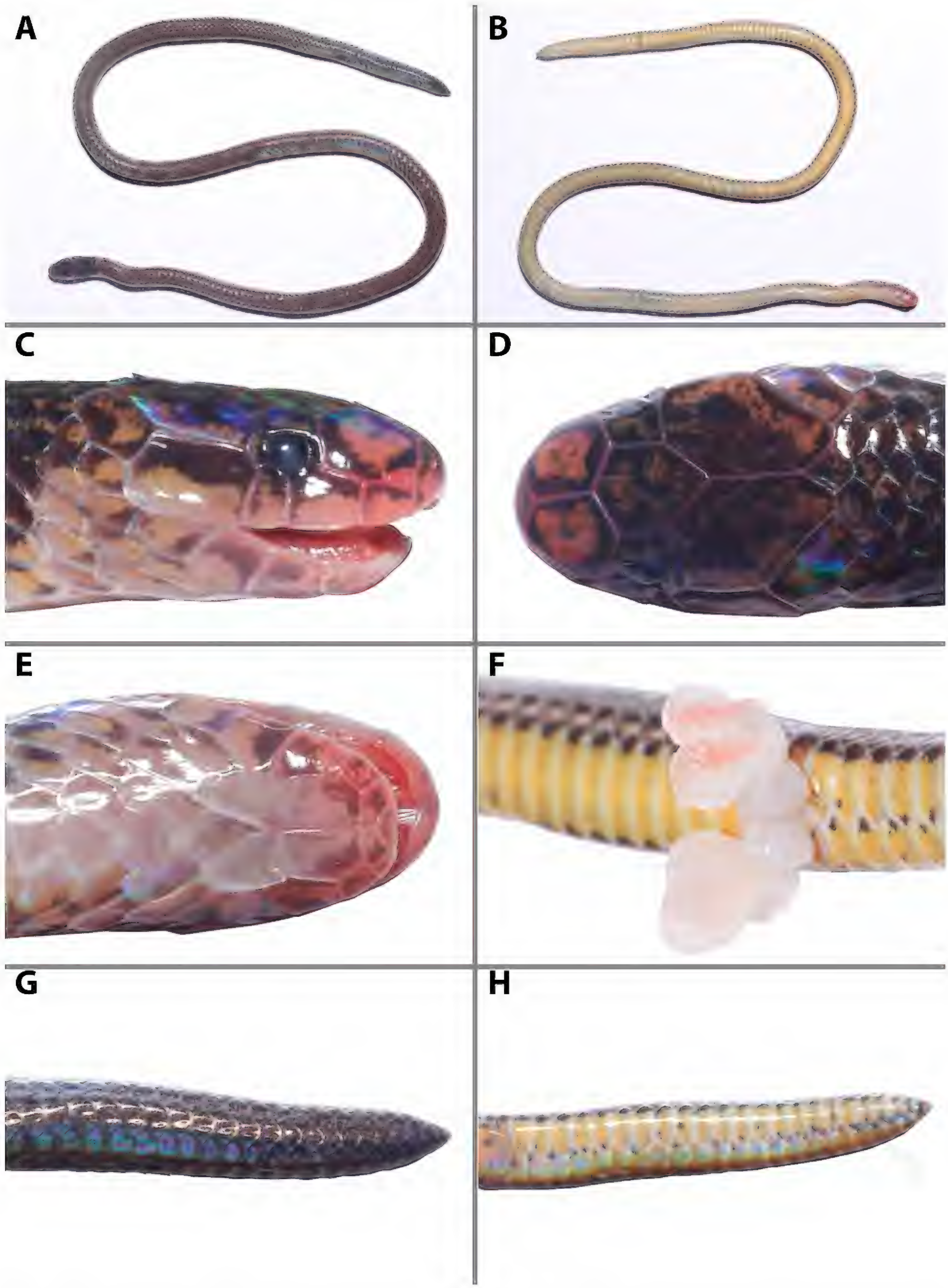

Figure 6. *Calamaria incredibilis* sp. nov., adult male (GEP r093, paratype) after euthanasia. **A.** Dorsal view of body; **B.** Ventral view of body; **C.** Lateral view of head, left side; **D.** Dorsal view of head; **E.** Ventral view of head; **F.** Cloacal region, showing the everted hemipenis; **G.** Dorsal view of tail; and **H.** Ventral view of tail. Photographs by ZCZ.

of light blotches on the neck (vs. absent). *Calamaria incredibilis* sp. nov. differs from *C. annamensis* by having a slightly longer relative tail length in males (TaL/TL 8.2–8.4% vs. 6.6%), and yellowish-white ventrals (vs. light orange to salmon with small black spots). The new species can be distinguished from *Calamaria arcana* by having yellowish-white ventrals (vs. orangish-red), the presence of light blotches on the neck (vs. absent), and the absence of a light blotch at the vent and two light blotches on each flank near the distal portion of the tail (vs. present). Finally, *Calamaria incredibilis* sp. nov. is distinct from *C. dominici* by having a dorsal coloration reddish brown to dark brown with narrow dark longitudinal stripes (vs. dark with irregular yellow blotches), the presence of light blotches on the neck (vs. absent), and yellowish-white ventrals (vs. dark with a few yellow blotches and bands).

Distribution, natural history notes, and conservation. *Calamaria incredibilis* sp. nov. is currently known from Ningming County, Chongzuo City, and Lingui District, Guilin City, Guangxi ZAR, China, with the two localities separated by more than 500 km, and is so far represented by only two specimens. Both specimens were collected during daytime surveys and were encountered on roads. Given the semi-fossorial habits of this species, it is likely to have a broader distribution within Guangxi. In addition, because the holotype was collected near the China-Vietnam border, we further hypothesize that this species may also occur in the Mau Son Mountain, Lang Son Province, northern Vietnam. At present, due to the very limited number of confirmed records and the lack of information on population size, trends, and threats, we recommend that *Calamaria incredibilis* sp. nov. be provisionally assessed as Data Deficient (DD) under the IUCN Red List criteria.

Discussion

The discovery of *Calamaria incredibilis* sp. nov. adds further evidence that populations historically assigned to *Calamaria pavimentata* in southern China do not represent a single widespread species, but instead comprise multiple independent evolutionary lineages. Recent integrative taxonomic studies have repeatedly demonstrated that the diversity of this group has been underestimated due to conservative external morphology, semi-fossorial habits, and historically limited sampling (Yeung et al. 2022; Cai et al. 2023; Zhang et al. 2025a; Qi et al. 2026). Collectively, these findings support the recognition of a *C. pavimentata* species complex rather than a single, morphologically variable taxon.

Within southern China, Guangxi ZAR emerges as a particularly important area for diversification within this complex. Several closely related species, including *Calamaria incredibilis* sp. nov., *C. jinggangensis*, and *C. similis* have now been documented from this region. Guangxi represents a biogeographic transition zone between southern China and northern Indochina and is characterized by extensive karst formations, pronounced elevational heterogeneity, and complex geological history. These factors likely promoted lineage isolation and subsequent diversification, resulting in the present-day occurrence of multiple closely related taxa within relatively restricted geographic areas.

The geographic proximity, and potential sympatry, of *Calamaria incredibilis* sp. nov. with other members of the species complex suggests that diversification within this group was not driven exclusively by strict allopatric isolation. Instead, historical range shifts followed by secondary contact, or diversification associated with fine-scale habitat heterogeneity, may have played an important role. Although ecological information on *Calamaria* remains scarce due to their secretive and semi-fossorial lifestyle, consistent morphological differences among closely related species—such as relative tail length, ventral scale counts, tail shape, and ventral coloration—may reflect subtle ecological differentiation. Such differences could be linked to variation in burrowing behavior, microhabitat use, or resource partitioning, potentially facilitating stable coexistence among congeners.

The recognition of *Calamaria incredibilis* sp. nov. also has important implications for the interpretation of historical records of *C. pavimentata* from southern China. Many earlier reports were based primarily on superficial morphological similarity and likely represent a composite of multiple distinct taxa. Therefore, all previous records of *Calamaria pavimentata* reported from China require critical re-evaluation using integrative taxonomic approaches that combine detailed morphological comparisons with molecular data. In particular, populations reported from areas adjacent to the confirmed distribution of *Calamaria incredibilis* sp. nov., including Jinxiu (Guangxi ZAR) and Wangmo (Guizhou Province), show certain morphological similarities to the new species in body size, tail proportions, and scale counts (see Table 3). However, historical records document a clear difference in the presence versus absence of caudal markings. Fan (1931) reported the presence of white spots on each side of the tail base in specimens from Jinxiu, whereas Wu et al. (1985) documented that some individuals from Guizhou exhibit such spots while others do not. This variability suggests that populations currently referred to *C. pavimentata* from Guizhou may not represent a single taxon, but potentially comprise more than one species. Consequently, the taxonomic status of these populations remains uncertain and should be regarded as provisional hypotheses pending confirmation based on the re-examination of voucher specimens and molecular data.

Despite the limited sampling, with only two specimens currently available, the congruence between diagnostic morphological characters and mitochondrial DNA evidence (cyt *b*) consistently supports the recognition of *Calamaria incredibilis* sp. nov. as an independent

evolutionary lineage. The observed combination of stable morphological differences and substantial genetic divergence from all congeners provides sufficient evidence for species delimitation under an integrative taxonomic framework, particularly in a morphologically conservative lineage such as *Calamaria*.

Future research should prioritize increased sampling across southern China and adjacent regions, especially in Guizhou and Hunan provinces of China and in northern Vietnam, where additional populations referable to *Calamaria incredibilis* sp. nov. or other undescribed members of the *C. pavimentata* species complex may occur. The incorporation of nuclear genetic markers, together with ecological and behavioral data, will be essential for clarifying species boundaries, assessing intraspecific variation, and reconstructing the evolutionary history of this group. Overall, the discovery of *Calamaria incredibilis* sp. nov. underscores the importance of integrative taxonomy for revealing hidden diversity in morphologically conservative, semi-fossorial snake lineages and confirms Guangxi as an important hotspot of cryptic diversification in southern China.

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